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Royal Institution of Great Britain.

WEEKLY EVENING MEETING,

Friday, April 25, 1873.

SIR HENRY HOLLAND, Bart. M.D. D.C.L. F.R.S. President,
in the Chair.

C PROFESSOR W. H. FLOWER, F.R.S.

On Palaeontological Evidence of Gradual Modification of Animal Forms.

I NEED scarcely say that one of the greatest, if not absolutely the greatest problem which has ever exercised the minds of naturalists is that of the fixity or the mutability of species.

Are the various specific forms under which animal and vegetable life exist upon earth, now and in all times past, fixed within certain narrow limits of variation, and did each originally appear upon the earth without genetic connection with any previously existing forms, having been created *de novo* in fact? or have these different species been produced by gradual modification from pre-existing living forms, under the influence of certain laws, at present very imperfectly understood, acting through vast and indefinite periods of time?

It is clear that these two views are strongly opposed to each other. Both have been held and still are held by men who are justly considered masters in the branch of knowledge to which they relate; and the solution of the question will exercise so important an influence on the progress of zoology that any real contribution towards it should be one of the most welcome additions to science that a naturalist of the present day can make.

The question is, indeed, so far-reaching, so all-pervading, that it meets us everywhere in the study of every group of animal or vegetable life, and in almost every aspect in which the study can be carried out.

It bears largely upon, and is greatly illustrated by, descriptive zoology or botany. It adds vastly to the interest of the pursuit of anatomy, by calling out the meaning of rudimentary structures and so-called typical resemblances; it elucidates obscure questions relating to the habits and instincts of animals; it brings into prominence the significance of various facts of geographical distribution, and the life it throws into the study of palaeontology is too obvious to need remark.

Evidences bearing upon, either for or against, the theory of *evolution* or *descent* can be collected from all these sources. I need only refer to Mr. Darwin's works, which must be familiar to you all,

in illustration of the great variety and number of the branches of science which can be brought to throw light upon it. Indeed, in a subject like this, where direct observation can count for little, in consequence of the extreme shortness of the observing time of any individual compared with the enormous period required for the assumed changes, it is only by the accumulation of a vast number of facts from various sources, and observing the direction in which they all point, that anything like proof can be obtained.

Leaving aside, for the present occasion, all other sources of evidence in favour of either of these views, I propose this evening to enter only upon one which is in some respects, as all must admit, the most important, as it comes nearer than any other to show what actually has been the history of our existing species in times past; for as the most natural and conclusive way of ascertaining the method by which a nation has arrived at its present condition of society, customs, laws, &c., would certainly be to examine into the preserved records of its past history, so it must be with the present condition of animal and vegetable life.

We all know that such records have been preserved, that the solid rocks beneath our feet in many places teem with the actual remains of creatures which lived and died, thousands or millions of years ago.

Why should they not yield to us the knowledge we are all so eager to acquire?

If species are and ever have been immutable, shall we not find the same hard and fast lines surrounding each as we do now? Shall we not find long series of similar forms following without change on an abrupt commencement? If the other alternative be correct, ought we not to find specimens of all the various stages through which the wonderful variety we meet with now has been brought about? Every gap which now so widely separates group from group ought to be filled up, and the various phases of modification should follow through the successive eras of geological time.

Now, there can be no hesitation in saying that the evidence of palæontology, in the present state of the science, does not reveal the last-described condition of things. Notwithstanding the vast increase of our knowledge in recent years, very many large groups of animals stand completely isolated, and the more nearly allied forms are mostly separated from each other by tolerably definite intervals.

Is, then, the question decisively answered against evolution or derivation by palæontology?

We must pause before we can join in the assertion that it is. The subject is far more complex than it may seem at first.

Before going further, a proper estimate must be arrived at of the nature and value of our evidence, and in doing this we must give full weight to the considerations derived from the "imperfection of the geological record" so strikingly elucidated in Mr. Darwin's chapter on the subject.

To those who have not fully considered this question, it is difficult

to conceive how immense is the interval between our excessively fragmentary knowledge of extinct animals, and that perfect palæontological record which would imply evidence, first, of every form of life that has ever existed, and, secondly, of the period at which it existed.

If there were time, I might dwell long upon this part of the subject, but I must leave you to imagine, I. What the chances are against the fossilization of any animal that dies. II. What the chances of the stratum in which some fossil remains have been embedded being itself preserved during the constant changes going on on the earth's surface, and ultimately appearing in a situation accessible to man's research. III. What the further chances against their being so found, even if they should have been preserved in an accessible locality.

I might refer you to the exceedingly minute portion of the earth's surface which has yet been really explored palæontologically; to the cases that are occurring every day of new and most unexpected forms and of whole species or orders, known only by an isolated individual, as the *Archæopteryx* of the Solenhofen oolite; to say nothing of more recondite speculations in the work above referred to, on the improbability of preservation of intermediate forms, owing to variation having usually been most rife during periods of elevation, when fossilization is less likely to occur.

All these show in such a striking manner the extremely little value of negative evidence in palæontology, that I am quite justified in asking you never for a moment to leave it out of consideration in thinking of, or reasoning on, what is to follow.

Such being the material with which we have to deal, it will be seen that we must go to work upon it in a most careful and circumspect manner. We cannot rush at conclusions, but must be content cautiously, and often with much labour and anxiety, to piece together our facts, scrupulously observing the minutest hints, and following out the direction indicated by often very obscure signs, before we can reconstruct even an outline of the fabric from which we hope to gain an idea of the past history of the beings of which we treat.

I have selected for illustration of the subject this evening the division or order of Mammals called by naturalists UNGULATA, or hoofed animals, chiefly because it is the one of which the palæontological history—at least in the tertiary period (for beyond that we cannot trace it)—is better known than any other, and as that of which the classification,—that is, the relations of its various sub-groups to each other,—is on the whole better understood than in most other zoological divisions.

The order includes the most familiar of our domestic animals, and with the general appearance of the rest we are most of us well acquainted, thanks to the Zoological Gardens. They are the various forms of horses, asses, and zebras, the rhinoceroses and the tapirs, the pigs, hippopotamus, camels, deer, antelopes, sheep, oxen, and goats.

They are essentially herbivorous (though some few may be more or less omnivorous), and their teeth are modified accordingly. Their

limbs are adapted for carrying the body in ordinary terrestrial progression, and are of very little use for any other purpose, such as climbing, seizing prey, or carrying food to the mouth. They never have clavicles or collar-bones, and their toes never exceed four in number (the digit which corresponds to the first of the complete pentadactyle foot being always wanting), and have the ends encased in hoofs instead of nails or claws. The species at present existing are very numerous, and widely diffused over the earth's surface, being wanting only in the Australian province. These Ungulate animals are divided into two natural groups, each having very many characters in common, the establishment of which, though contrary to the views of the great naturalists at the beginning of this century, has been a great gain to zoological science, especially as this division pervades all the known extinct as well as recent forms; and although some forms of either group may present some partial approximation to the other, no directly intermediate species are known. It is important, therefore, to apprehend thoroughly the distinction between these groups, which have received from Professor Owen the names of *Perissodactyle*, or odd-toed, and *Artiodactyle*, or even-toed, from one of their most striking external characteristics. The first have the toes of both feet arranged symmetrically to a line drawn through the middle of what would be the third toe of the typical pentadactyle foot, which too is always the largest, and in some cases the only one fully developed. In the second, the toes are arranged symmetrically to a line drawn between the third and fourth toes, so that these two toes are equally developed, and may be alone present, or may be supplemented by an outer pair (the second and fifth), often in a more or less rudimentary condition. Besides these distinctions in the limbs, there are so many others correlated with them in the number of the vertebræ, the structure of the cranial bones, of the teeth, of the digestive organs, &c., that there can be no question about their forming natural divisions, very important to palæontologists, as it often happens that the position of an extinct and little-known form can be determined from a very small fragment of bone.

Each of these groups is further divided into genera, the names of which in what appears, in the present state of knowledge, to be their natural position and relation to each other, are indicated on the diagram. From this, it will be seen, that the existing Perissodactyles (excluding Hyrax, the position of which is doubtful, though I am inclined to consider it as an aberrant member of this group) consist of three groups, the tapirs, the rhinoceroses, and the horses, each represented by but few species, and (except in the case of the horse, through the agency of man) of rather restricted geographical distribution.

These groups at present are separated by very decided intervals, so much so, that one of them, containing the horses, has been considered by many naturalists as forming an order apart, the *Solidungula*.

The existing Artiodactyles range themselves around two principal types, the tubercular-toothed, or bunodont, and the crescentic-toothed,

or selenodont.* To the former belong the pigs in all their modifications, including the babirussa and wart-hogs, and the hippopotamus and peccary. To the latter the ruminants, *i. e.* vast numbers of species of animals included under the general designation of sheep, oxen, goats, antelopes, deer, musks, giraffes, and the two allied though aberrant forms, the camels, and the *Tragulidæ* or chevrotains, an interesting little group long confounded with the musk deer.

The two extremes of this division, represented by the pigs and the hollow-horned ruminants, seem to have very little in common at first sight, and if we were acquainted with the organization only of the existing species, we might be justified in treating them as belonging to very distinct groups. But even among existing forms there are some examples, which may almost be called intercalary types, so widely do they depart from the group to which they are most nearly relative in the direction of the other.

These are among the bunodonts, the little South American peccaries (*Dicotyles*), and among the selenodonts, in a far greater degree, the chevrotains (*Tragulus*). The latter in many remarkable characters deviate strongly from the ruminants, and approach the pigs, or rather, as will be shown presently, to the generalized type of the entire group.

Such being the present condition of the order, what does palæontology reveal of its past history?

In the first place, it is most necessary to bear in mind the provisional character of all classifications of extinct animals, because of our imperfect knowledge of their structure; but endeavouring to make the best use of what little we possess, I have added in the diagram all the best known extinct forms somewhere near the position, in relation to the existing forms and each other, in which their affinities would place them; and by the different colours their relation as regards time is shown.

The tertiary period, with which we are now alone concerned, has here been divided for convenience into six epochs. Of course, it were possible to have gone into minute details and made many more divisions, but it would have made the diagram less clear, and it is best, perhaps, not to attempt to refine too much in this somewhat tentative exposition of a biological history, especially as there is still much uncertainty as to the exact relative age of many of our fossiliferous strata.

The epochs chosen are the recent (including the pleistocene), the pliocene, late and early miocene, and late and early coeue, each represented by a different colour. It is not meant that if a genus or group is here assigned to one of these epochs, that some of its members may not have extended in some degree beyond its limits (as it must be always remembered that the boundaries of these epochs

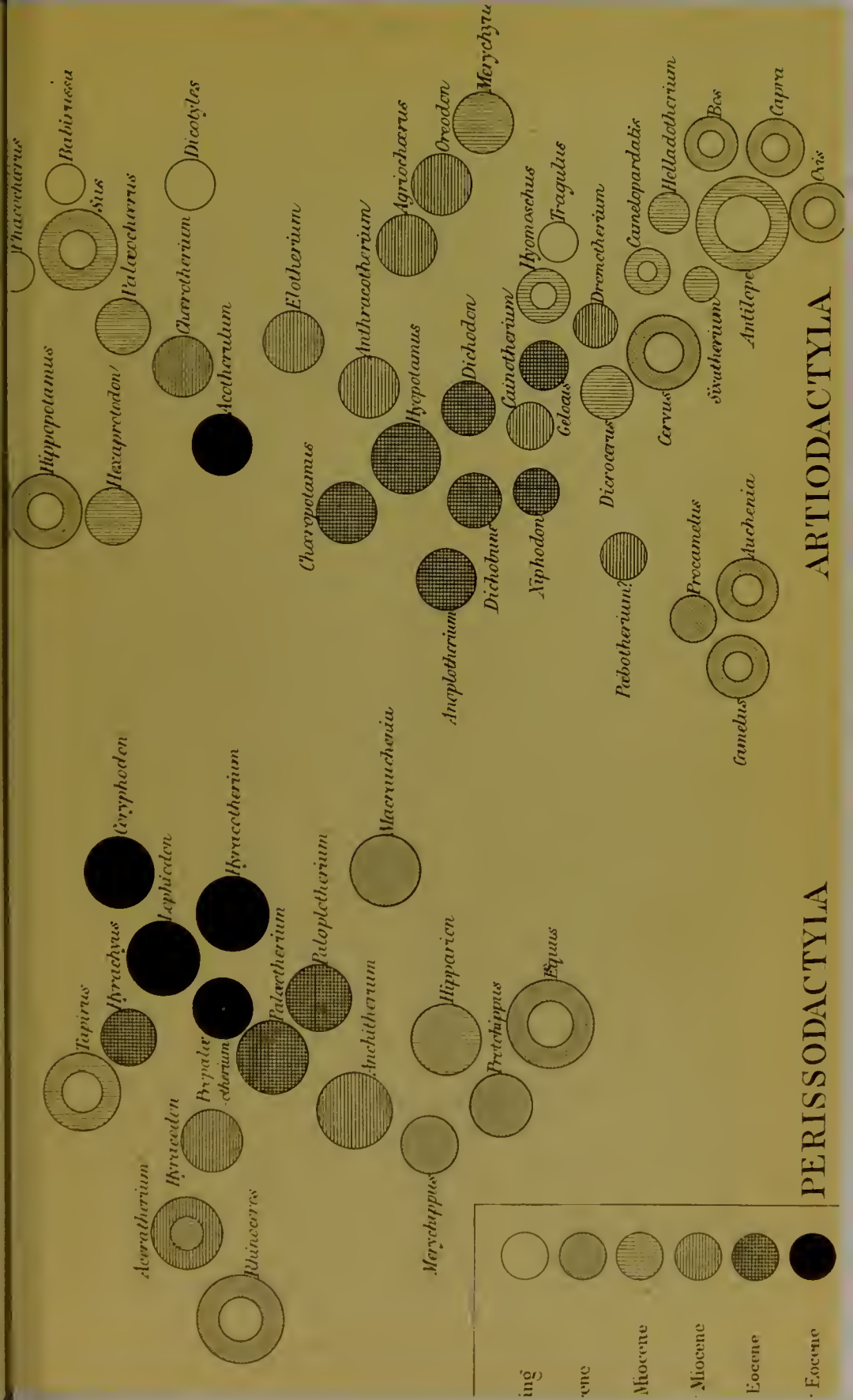
* I borrow these convenient terms from a paper lately read before the Royal Society by Dr. W. Kowalevsky.

are quite artificial), either before or after, but that the period assigned to it was that in which it most chiefly flourished. When two colours are represented, one within another, it signifies that the group existed in both, and of course in all intervening periods.

To begin with the Perissodaetyles. The earliest known forms constitute a family called *Lophiodontidæ*, composed of the genera *Lophiodon*, *Coryphodon*, and *Hyracotherium*. Of these animals little is known except the teeth, which however indicate rather a primitive or root form, from which, by modification, all the other teeth of Perissodactyles can be derived. The elevations and depressions of the molar teeth of *Lophiodon*, for instance, are arranged on a pattern which is the best key to that of all others of the sub-order; and it is by going back, as it were, to it, that we can understand and compare all the other variously modified, and often more complicated, forms. Moreover, these Lophiodonts possess a dental character which distinguishes them from all other *Perissodactyles*, and brings them into a more generalized ungulate type, for which reason I place them nearest to the earlier forms of artiodactyles—that is, that all the premolars are smaller and of a simpler form than the true molars. Whether they possessed any modification of the limbs or other structures which bear them out in this position, we unfortunately cannot say.

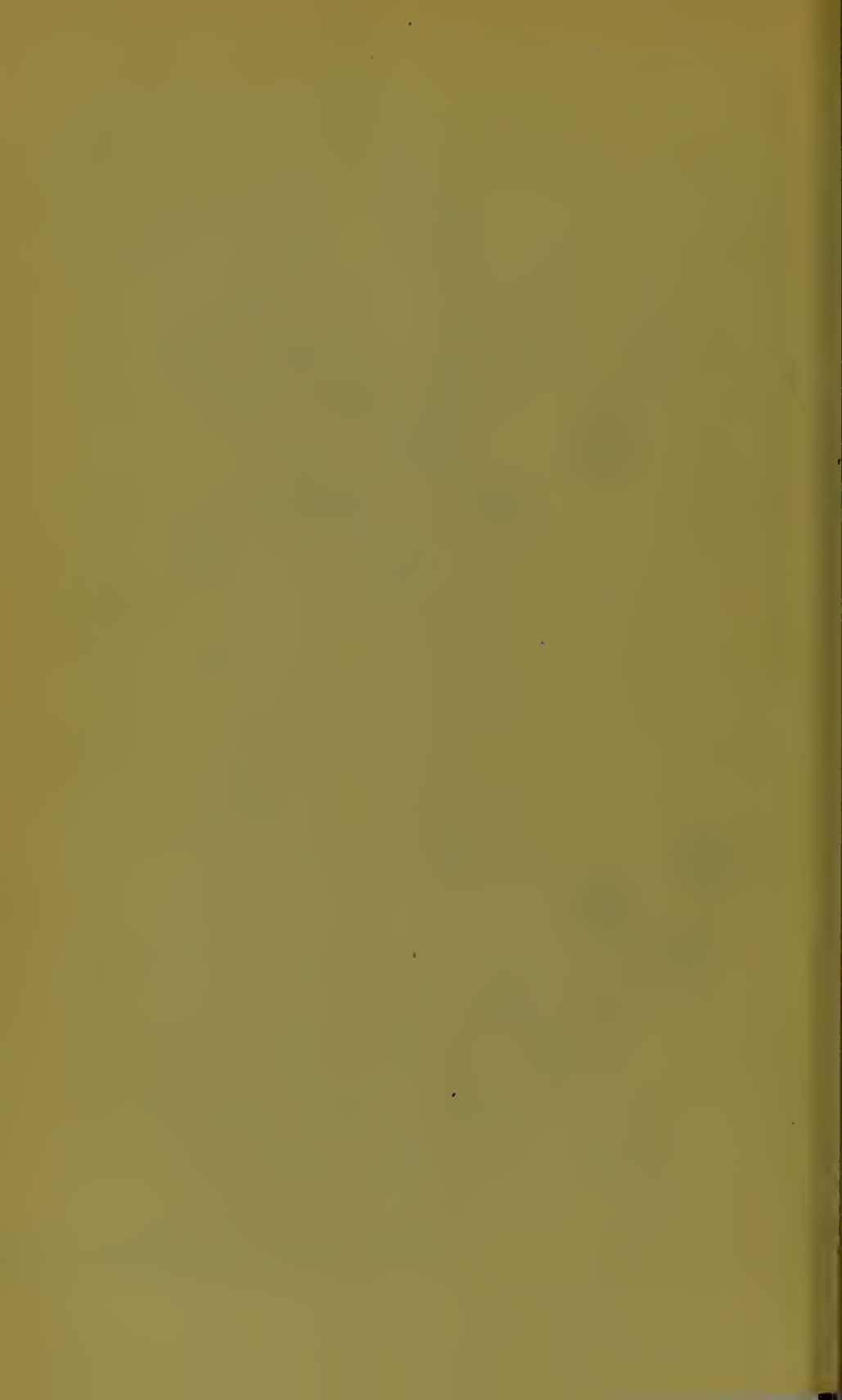
At a somewhat later epoch in the earth's history appeared on the scene the *Palæotheriidæ*, an important group, containing animals the osseous structure and dentition of which are completely known, chiefly through the famous researches of Cuvier into the fossils found in the gypsum quarries at Montmartre. These were animals something like existing tapirs, with three toes on each foot, complete and distinct radius and ulna and tibia and fibula, complete typical number of teeth, *i.e.* $i \frac{3}{3} c \frac{1}{1} p \frac{4}{4} m \frac{3}{3} = 44$; but the molar teeth modified in pattern from that of the Lophiodonts. They flourished in the later eocene, after which period they are no longer met with. They have been divided into several genera, but Gaudry has shown that these are united by transitional forms, and present a gradual series of modifications, corresponding with successive geological epochs.* Another offset, from the ancient Lophiodont stock (with which it appears to be connected through the American eocene *Hyracahyus*), constitutes the family *Tapiridæ*, first known in the miocene and continued with scarcely any modification to our own day, and therefore a most interesting form to contemplate in its living state, as it brings back, in the most striking way, the general facies of the fauna of those ancient times. In one respect the tapir is remarkable among Perissodaetyles, as it has on its fore feet as many as four toes, thus retaining a primitive or generalized character. The other two existing forms, the rhinoceros and the horse, appear to be more direct modifications of the *Palæotherium* type, though in different directions. The existing

* 'Remarques sur les Palæotherium,' Nouv. Archives du Muséum d'Histoire naturelle, tom. i., 1865, p. 15.



PERISSODACTYLA

ARTIODACTYLA



rhinoceros closely resembles the Palæotherium in the general structure of its skeleton, limbs, number of toes, &c., and in the general pattern of the molar teeth; it differs, however, in the greatly reduced number of front teeth, incisors and canines, which in the African two-horned species are often absolutely wanting; and also in the possession of those singular epidermal appendages to the face, the well-known horns, either one or two in number. Now palæontology points out with tolerable precision the intermediate steps by which these modifications have been brought about. A small ancient rhinoceros has been found in the early miocene of North America, to which Leidy has given the name of *Hyracodon*, which had no horn, and had the complete number of incisor and canine teeth, and was in many ways, at least as far as the skull and teeth are concerned, intermediate between *Palæotherium* and *Rhinoceros* proper. The earlier known European rhinoceroses have had the name *Aceratherium* given to them, the small size of the nasal bones being apparently quite unfitted to support such a weapon as a horn. The resemblance of their skull to *Palæotherium* has been pointed out by H. v. Meyer.

The more recent fossil rhinoceroses present wonderfully intermediate forms between some of the existing species, as *R. pachygnathus*, of Pikermi, as Gaudry has shown, is about equally related to the two species of modern African rhinoceros, and might have been (upon the derivative hypothesis) the ancestor of both. In the same way the Himalayan *R. sivalensis* appears to be related to the modern *R. indicus* and *sondiacus*, and the *R. schleirmacheri* to the Asiatic two-horned species. One special line of variation indicated chiefly by the ossification of the nasal septum culminated in the *R. tichorhinus*, which became extinct only in the most recent geological epoch. The history of this small group alone in its bearings upon evolution, might occupy many lectures; I must content myself now only with one observation, borrowed from Mr. Boyd Dawkins, that in all modern rhinoceroses the molar teeth have deeper crowns than in those which existed prior to a certain epoch, so that the height of these teeth alone will serve to distinguish a pleistocene from a pliocene form, in other respects closely allied. The value of this observation will be illustrated in the sequel.

The next line of modification from *Palæotherium*, is that which culminates in the most specialized of mammals, the modern horse, an animal we are so accustomed to look at that we scarcely ever notice the most remarkably adaptive character of its structure for its special mode of life. If we were not acquainted with the horse (and here of course I include its immediate allies, the asses and zebras,) we could scarcely conceive of an animal whose only support was the tip of a single toe on each extremity, to say nothing of the singular conformation of its teeth and other organs. So striking have these characters appeared to many zoologists, that the animals possessing them have been reckoned as an order apart called *Solidungula*; but palæontology has revealed that in the structure of its skull, its

teeth, its limbs, the horse is nothing more than a modified *Palæotherium*; and though still with gaps in certain places, many of the intermediate stages of these modifications are already known to us, being the *Paloplotherium*, *Anchitherium*, *Merychippus*, and *Hipparion*. On this very interesting point, which looks more like a real genealogical history than any other known, however, I need not dwell, as it was so fully treated of in a lecture delivered in this theatre three years ago by Professor Huxley—a lecture entitled the “Pedigree of the Horse.”

Lastly, there is *Macrauchenia*, a curiously modified Perissodactyle found in pleistocene times in South America, apparently another derivative of the palæotherium type, presenting resemblance (though perhaps only analogical) to some of the artiodactyles, especially the camels.

Directly intermediate forms between *Macrauchenia* and the other animals of its group are not yet known; but considering how little evidence we have of the animal life of the middle or older tertiary of South America, this is not to be wondered at.

On the whole it will be seen, that taking actual anatomical characters alone, palæontological research, even so far as it has yet been carried, bridges over most of the gaps existing between the modern form of Perissodactyles, entirely abolishing for instance the order *Solipedia*, as it is impossible to draw a satisfactory line where the animal ceases to be equine and becomes a palæotheroid; some drawing it between *Anchitherium* and *Palæotherium*, some between *Anchitherium* and *Hipparion*. Moreover, and this is most important, the lines from the modern more specialized forms converge towards the ancient more generalized forms; so that if we could get a side-view of what is shown in the diagram, the earliest forms at the bottom and the latest at the top, we should have lines (broken it is true, here and there) diverging from a common, or near a common centre, towards a circumference above—a view, in fact, of the conventional genealogical tree.

We turn now to the *Artiodactyles*, represented at present by the scattered groups before spoken of, clustering round two type forms so widely sundered in their structure and habits as the pig and the ox; but the former history of this division yields a totally different state of things. Of early cocene Artiodactyles we know very little at present; but in the later divisions of the same epoch forms appeared, such as *Anoplotherium*, *Dichobune*, *Chæropotamus*, and *Hyopotamus*, which were certainly neither pigs nor ruminants, but which partook remarkably of the characters of both. They had the complete number of teeth, *i.e.* incisors and canines, like modern pigs, but molars with indications of the crescentic pattern so characteristic of ruminants. They had two or four toes; but the metacarpals and metatarsals were not united to form a cannon bone as in ruminants, and they wanted the horny appendages to the head, so usually met with in the modern representatives of that group. From some of these central forms, or more probably from a

still earlier allied group indicated by the genus *Acotherulum*, or by some other still undescribed remains from Manremont, transitions can be traced with few breaks, through the successively modified miocene genera *Chærotherium* and *Palæochærus* to the genus *Sus*, or true pig, in which the dentition undergoes some remarkable specializations, as the upturning of the upper canines, and great development and extremely tuberculated character of the posterior molars, which are both singularly exaggerated in some modern offsets of the pig family, the first in the babirussa, and the second in the wart-hog (*Phacochærus*). More distantly related to the true pigs are the hippopotamus on the one hand, and the peccary on the other. In relation to the first, not found anteriorly to the latest miocene, it is significant that the earliest known forms had the more generalized number of incisor teeth (six) instead of four as in the modern hippopotamus, and hence has been made into a genus by itself, called *Hexaprotodon*.

The researches of Leidy into the ancient (miocene and early pliocene) fauna of Nebraska have furnished evidence of a remarkable group of animals now entirely extinct, the *Oreodontidæ*, the characters of which are perfectly intermediate between those of the pigs and the ruminants; animals with pig-like feet and complete number of incisors, canines, and molars, but with the latter important set of teeth, formed precisely on the same type as those of the deer. Within this particular group Leidy has noted a curious series of slight modifications coinciding with the successive age of the strata in which the remains were found. *Agriochærus*, the most ancient, approaches nearer to *Chæropotamus*, has orbits open behind and very shallow-crowned teeth. Then follows *Oreodon* proper, and lastly *Merychys*, more like the modern ruminants.*

To return to the European forms, in the genus *Gelocus*, where the union of the two principal bones of the metapodium first occurs, Kowalevsky has noticed the gradual way in which this change seems to have been brought about in successive epochs of cocene and early miocene strata, at first free in the young, and only coalescing in old animals, afterwards coalescing at a much earlier age. The gradual perfecting of the foot by the development of the ridge round the lower articular end of the metapodium in later forms, the ridge being quite wanting in early forms of the same group, has been noticed by the same author in many different series of Ungulates.†

During the miocene period the peculiar dental characteristics of the modern ruminants, especially the loss of the upper incisors, were developed, all sclenodont artiodactyles henceforth showing it. Of this early race of imperfect ruminants, still retaining many generalized characters, especially in the skull, the cervical vertebræ, fibula, stomach, &c., the chevrotains (*Traquilidæ*) are the survivors, especially

* 'The Extinct Mammalian Fauna of Dakota and Nebraska,' 1869.

† See also his interesting observations on adaptive and inadaptive modifications of the feet.—*Proc. Roy. Soc., Feb. 6th, 1873.*

the West African *Hyomoschus*, which has existed almost unchanged since the late miocene of Sansans and Steinheim. Then for the first time the appendages called antlers were introduced, but only in a comparatively rudimentary condition, with long pedicles and few branches, as in the modern Muntjaks. It was not till pliocene and especially pleistocene epochs that the wonderful and luxurious variety of cervine antlers reached their full development. As offshoots of the deer group, the giraffe, the gigantic Siwalik *Sivatherium*, and the *Helladotherium* of Greece may be mentioned, the two latter having become extinct, apparently without descendants.

Later still, the yet more specialized forms of hollow-horned ruminants appear—forms which now dominate the earth, being of all Ungulates the most widely diffused and most numerous in species, in individuals, and in outward variety, though in essential structure all alike. One of their principal characteristics is the modification of their molar teeth in the same way as in the modern horses, to which in some respects they seem to form a parallel group. The difference between the molar tooth of a hollow-horned ruminant and that of a deer consists in the great lengthening of the crown without any change in the pattern of the enamel folds, and in the addition of cement to support these folds. This alteration did not take place suddenly, and the crowns of teeth of the artiodactyles before the time of deer were still shorter than in those animals.

Among the deer themselves, as Lartet observed,* the most ancient have very short-crowned molars, and the depressions on the surface are so shallow that the bottom is always visible, while in the Cervidæ of the more recent tertiary periods, and especially the pleistocene and living species, these same cavities are so deep that, whatever be the state of dentition, the bottom cannot be seen. This (he says) is a perfectly reliable rule for distinguishing the ancient from the more modern forms of deer, and can be applied to other animals as well as the Cervidæ. From it he surmises that the duration of the life of modern is greater than that of ancient deer. The same careful observer also remarks that a gradual progress is observed in the volume of the brain and complexity of its surface, as deduced from casts of the interior of the skull, from which fact he concludes that a gradual growth of vital energy and intelligence has occurred as the effect of the tendency of animated nature towards improvement, of which the cause is always acting, and the limits indefinite.

Thus the history of the Even-toed Ungulates tells the same story as that of the Perissodactyles. The modern forms are placed along lines which converge towards a common centre. Moreover, the lines of both groups, to a certain extent, approximate; but within the limits of our knowledge they do not meet. Both artiodactyles and perissodactyles existed low down in the eocene, just as Carnivores,

* 'Comptes Rendus,' 1868, tom. 66, p. 1119.

Insectivores, bats, rodents, and other great groups then existed with boundary lines as distinctly marked as now.

Was the order, according to which the introduction of new forms seems to have taken place since that epoch, then entirely changed? or did it continue as far back as the period when these lines would have been gradually fused into a common centre?

Here we are landed in the region of pure speculation; but bolder travellers than I have endeavoured to penetrate its mysteries, as may be seen by a perusal of Professor Huxley's presidential address to the Geological Society for 1870.*

I have so far confined myself within the region of the known, and shown that at least in one group of animals the facts which we have as yet acquired point to the former existence of various intermediate forms, so numerous that they go far to discredit the view of the sudden introduction of new species.

They show also many cases of gradual modification of particular organs, probably always to the benefit of the race, and also a general progress from lower to higher or more specialized types; though, as in all other cases of progress (human civilization, for instance), attended with many exceptions, some local and temporary, some only apparent.

Whether the inferences which seem to me to follow from these facts are true or not, may still be an open question; for the sake of the stimulus that an open question of this sort lends to scientific research I am very glad that it is so; but if true, if we are led by them to the conclusion that the world we live in is a world of gradual growth and progress, and orderly evolution, what grander view of the Creation and the history of that world can we have opened to us?

[W. H. F.]

* Republished in his 'Critiques and Addresses,' 1873.

